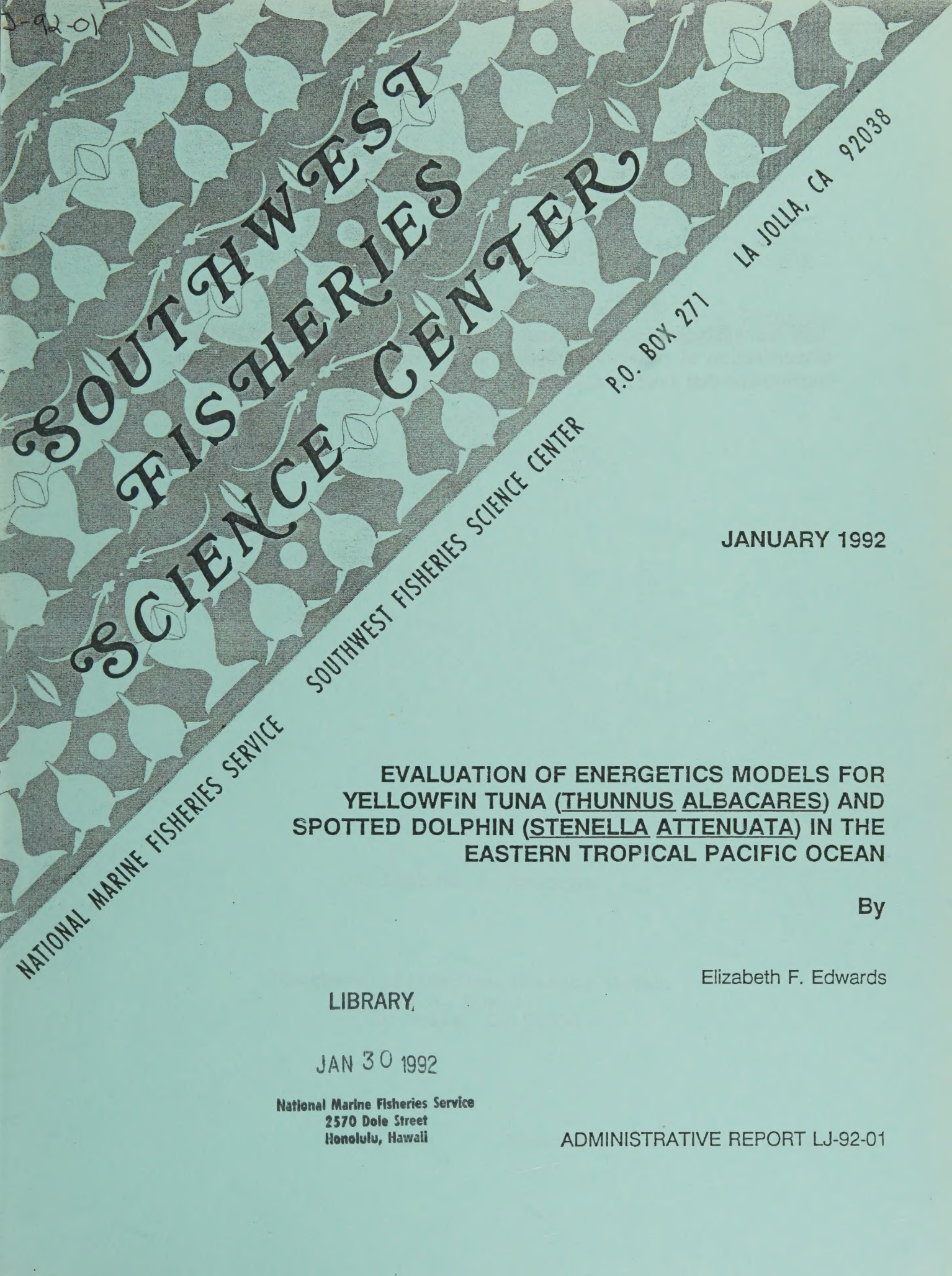




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JANUARY 1992

EVALUATION OF ENERGETICS MODELS FOR
YELLOWFIN TUNA (THUNNUS ALBACARES) AND
SPOTTED DOLPHIN (STENELLA ATTENUATA) IN THE
EASTERN TROPICAL PACIFIC OCEAN

By

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ADMINISTRATIVE REPORT LJ-92-01

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Evaluation of energetics models for yellowfin tuna (Thunnus albacares) and spotted dolphin (Stenella attenuata) in the eastern tropical Pacific Ocean.

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Administrative Report LJ-92-01

ABSTRACT

Evaluations are presented for bioenergetics models of yellowfin tuna (Thunnus albacares) and spotted dolphin (Stenella attenuata) in the eastern tropical Pacific Ocean. The models estimate daily energy flow (in calories) through all sizes of individuals in a typical tuna-dolphin association. Estimates of energy fluxes (ingestion, active and standard metabolism, heat of digestion, egestion and excretion) fall within acceptable, expected ranges when the most apparently reasonable values are used for energetics parameters.

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INTRODUCTION

Bioenergetics models (Kitchell et al 1977) are presented for yellowfin tuna (Thunnus albacares) and spotted dolphin (Stenella attenuata) occurring in mixed associations in the eastern tropical Pacific Ocean. Because neither model can be verified directly by physiological measurements (as neither the large yellowfin nor the spotted dolphins have ever been kept successfully in captivity nor have experiments in situ been possible), 2 indirect approaches have been used instead to evaluate the efficacy of the models: 1) comparisons of estimated physiological rates with values that have been measured in similar animals, and 2) comparisons of the relative importance (proportions of total energy flux) of various processes as predicted by the models, with theoretical or observed importance. Results are presented for each model in turn.

Yellowfin Tuna Energetics Model

The model developed here addresses only those sizes of yellowfin found associated with dolphins. These tend to be relatively large Age II and Age III fish (55-85, and 85-125 cm fork length (FL) respectively).

The model for individual yellowfin follows the standard bioenergetics approach, balancing food requirements against estimated energy costs for metabolism and energy savings as growth in biomass (University of Wisconsin Sea Grant 1989). Ambient water

temperature was held constant at 27C, as most of the tuna-dolphin habitat occurs in waters of this temperature.

Specific rates of consumption, cost of swimming (active metabolism), standard metabolism, heat of digestion, and waste energy losses (excretion and egestion) were estimated for individual tunas as a function of size. Rates of energy flux for yellowfin schools were estimated as the sum of weight-specific estimates for individuals in the group. Based on catch records from the fishery, an "average" association was assumed to include 500 yellowfin with an age composition of 65% age II and 35% age III fish per school (Mullin¹)

The Wisconsin bioenergetics model derives estimates of energy flux by iteratively fitting an energetics equation for growth in body weight over time, to observed growth rate curves derived from field samples of the organism in question. The tuna model used as the calibration growth curve the Gompertz fit derived by Wilde (1986) for yellowfin tunas from the ETP. When necessary, body lengths (FL; fork length in centimeters) were converted to weights (WW_g; wet weight in grams) using the length-weight relationship²

¹Mullin, A. 1986. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038. unpubl. data from commercial fishery.

²unpubl. data for yellowfin tuna from the ETP; A. Wilde, Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, Ca. 92038

$$FL = e^{((\ln(WWg/1000)+11.184)/3.08612)}$$

Specific rate of consumption (C_{sp} ; calories food consumed · calories animal⁻¹ · day⁻¹) by yellowfin was estimated as

$$C_{sp} = C_{max} * P_{val} * F(T)$$

where C_{max} is maximum possible consumption for the largest yellowfin, P_{val} is an iteratively fitted value in the range 0-1 that when "correct" results in the simulated growth curve matching the observed growth curve (University of Wisconsin Sea Grant 1989).

$$C_{max} = C_a * WW_g^{C_b}$$

where $C_a^3 = 1.2$ and $C_b^4 = -0.22$.

$F(T)$ is a function describing the effect of temperature on feeding rates. The yellowfin energetics model used Consumption

³based on the assumption that maximum feeding rate for very large yellowfin tunas (95000 g wet weight) wouldn't exceed 10% per day (i.e., $a = 0.10/(95000^{-0.22})$). In practice, the exact value chosen for C_{max} is flexible, as higher values simply reduce the fitted value of P_{val} , and vice versa.

⁴ by analogy to walleye, Kitchell et al. 1977.

Model #2 (for warm water fish) from the Wisconsin Model (Wisconsin Sea Grant 1989) for estimating $F(T)$, where

$$F(T) = V^X * e^{(X * (1-V))}$$

with

$$V = (T_m - T_a) / (T_m - T_o)$$

$$X = W^2 * (1 + (1 + 40 / Y)^{0.5})^2 / 400$$

$$W = \ln(Q) * (T_m - T_o)$$

$$Y = \ln(Q) * (T_m - T_o + 2)$$

T_m , T_o , and T_a are maximum, optimum, and ambient feeding temperatures, assumed to be 33C, 27C, and 27C, respectively, in the tuna model. The term Q approximates a Q_{10} for the rate at which the function $F(T)$ increases over relatively low temperatures⁵. This function increases from 0 (at low temperatures) to 1 at the optimum temperature and back to zero at the maximum temperature (verbatim; University of Wisconsin Sea Grant 1989).

Specific rate of respiration (R_{sp}) was estimated as

⁵ Q assumed = 2.0, based on Dizon and Brill (1979).

$$R_{sp} = R_t * F(T)$$

where total specific rate of respiration (R_t) is

$$R_t = (STD_w + ACT_w) * (20650 / CAL_{an})$$

with energy costs of standard (STD_w) and active metabolism (ACT_w) expressed in watts. The factor 20650 converts watts to calories·day⁻¹. Dividing by total caloric content of the animal (CAL_{an}) produces the specific rate.

Total caloric content of yellowfin was estimated as a function of wet weight

$$CAL_{an} = CD_y * WW_g$$

where caloric density of yellowfin tuna (CD_y) = 1440 calories·gram wet weight⁻¹ (Boggs 1984).

Energy cost of standard metabolism was assumed constant for all sizes of yellowfin (Boggs 1984) as

$$\text{STD}_w = 0.464 \text{ watts} \cdot \text{gram wet weight}^{-1}$$

Energy cost of active metabolism was estimated using Bogg's (1984) equations and data for energy costs of respiration in yellowfin

$$\text{ACT}_w = F * \text{VL}^G * \text{FL}^H$$

where VL is velocity in $\text{cm} \cdot \text{sec}^{-1}$ and $F (= 1.59 \text{ E}^{-4})$, $G (= 1.64)$, and $H (= -1.28)$ are fitted parameters derived from Bogg's (1984) laboratory studies on yellowfin energetics.

Yellowfin were assumed to swim at length-specific optimum sustained cruising speeds, with velocity scaling to fish length as

$$\text{VL} = \text{VL}_a * \text{FL}^{\text{VLb}}$$

where $\text{VL}_a^6 = 20.6$ and $\text{VL}_b^7 = 0.4$.

⁶Estimated based on 100 cm FL yellowfin swimming on average 130 $\text{cm} \cdot \text{sec}^{-1}$ in situ (Holland et al. 1990).

Specific rate of specific dynamic action (SDA_{sp}) was estimated as

$$SDA_{sp} = SDA * C_{sp}$$

where $SDA^8 = 0.15$.

Specific rate of waste losses (WL_{sp}) were estimated as the sum of fractional losses to egestion (F_a) and excretion (U_a)

$$WL_{sp} = (F_a + U_a) * C_{sp}$$

where $F_a = 0.20^9$ and $U_a = 0.07^{10}$.

⁷based on theoretical and empirical studies by Weihs (1973, 1981).

⁸ SDA is the fraction of yellowfin diet converted to heat energy during digestion. SDA was assumed = 0.15, reflecting the relatively high protein, low carbohydrate diet ingested by yellowfin tunas (Olson and Boggs 1986).

⁹ based on the relative assumed non-digestible portions of tuna diet items by analogy to similar items (Cummins and Wuycheck 1971).

¹⁰based on measurements of non-fecal excretion by carnivorous fish (Brett and Groves 1979).

Specific rate of growth was estimated as

$$G_{sp} = C_{sp} - (R_{sp} + SDA_{sp} + WL_{sp}).$$

Total grams wet weight biomass available daily for growth (G_{wwg}) is this specific rate times the weight of the fish, i.e.,

$$G_{wwg} = G_{sp} * WW_g$$

Correcting for the relative energy density (calories per gram wet weight) of both the prey (CD_f^{11}) and the yellowfin (CD_y), new wet weight on day (i) is

$$WW_{gi} = [(CD_y * WW_{g(i-1)}) + (G_{wwg(i-1)} * CD_f)] / CD_y.$$

¹¹Energy density of yellowfin food (CD_f) was based on an assumed constant diet of 70% fish, 20% squid, and 10% invertebrates (Olson and Boggs 1986), with undigestible fractions of 0.124, 0.066, and 0.250, and caloric densities of 1440, 1260, and 1000 calories.gram wet weight⁻¹, respectively. Average ingested energy density (including the undigestible fraction) is 1380 calories.gram wet weight⁻¹.

Energy costs of reproduction were not included in estimates of consumption, because the model focuses on the sizes of yellowfin associated with dolphins. These tend to be relatively immature fish. Spawning activity in yellowfin doesn't occur in fish much smaller than 80 cm, and increases slowly to the maximum activity in fish larger than about 150 cm (Joseph 1963).

Spotted Dolphin Energetics Model

As in the yellowfin model, specific rates of consumption, cost of swimming (active metabolism), standard metabolism, heat of digestion, and waste energy losses (excretion and egestion) were estimated for individual dolphins as a function of size. Rates of energy flux for groups of dolphins (i.e, for an average school) were estimated as the sum of estimates for individuals in the group.

Some of the energetics parameters reported here are based on morphological measurements from 4 dolphin specimens from the ETP; 3 spotted dolphins ranging in size from 81 to 189 cm total length, plus one spinner dolphin (Stenella longirostris) 114 cm in length. The 81 cm individual was a very-late term fetus carried by the 189 cm animal. Although this sample is very small, all morphological measurements from these 4 animals fall well within the bounds of size-related regressions of morphological characteristics derived subsequently for a sample of 34 spotted dolphins ranging in size

from 74 to 215 cm total length (tip of rostrum to fluke notch) (Edwards¹²).

The calibration growth curve for expected size at age was derived from equations and figures in Hohn and Hammond (1985) and Hohn¹³. Weight-length conversions assumed the relationship

$$WW_{kg} = 1.4 e^{-5} * TL^{2.95}$$

where WW_{kg} is wet weight in kilograms and TL is total length (tip of rostrum to fluke notch) in centimeters, based on weight-length measurements from a sample of 50 spotted dolphins ranging in size from 82 to 210 cm total length.

School composition was assumed to reflect the apparent age distribution of the spotted dolphin population, which in turn was assumed to appear as the length (age) distribution of dolphins collected during purse-seining operations in the ETP (Smith 1979, Barlow and Hohn 1984, Hohn¹⁴). Proportions of nursing calves (ages 0-2 year), adolescents (ages 3 - 14 years), sexually adult males (ages 15 and up), and sexually adult females (ages 11 and up)

¹²Edwards, E. F., Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038; unpubl. data.

¹³Hohn, A. 1985., Southwest Fishery Center, P.O. Box 271, La Jolla, CA. 92038. unpubl. data

¹⁴Hohn, A. 1985. Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038. unpubl. data.

in an average school were 0.05, 0.40, 0.25, and 0.30. Proportions of adult females not pregnant or lactating, lactating, pregnant, and pregnant and lactating animals were 0.05, 0.15, 0.08, and 0.02.

Specific rate of consumption (C_{sp} ; calories food consumed·calories animal⁻¹·day⁻¹) by individual spotted dolphin was estimated as

$$C_{sp} = \text{CONS}_{cal} / \text{CAL}_{an}$$

where

$$\text{CAL}_{an} = \text{CD}_d * \text{WW}_g$$

and

$$\text{CONS}_{cal} = \text{CONS}_{ind} * \text{CD}_f.$$

WW_g is dolphin wet weight in grams, CD_d is caloric density of

spotted dolphins¹⁵, CD_f is caloric density of food¹⁶, and $CONS_{ind}$ is grams wet weight of food consumed daily, estimated as

$$CONS_{ind} = C_{max} * P_{val} * WW_g$$

P_{val} is again an iteratively fitted value that when "correct" results in the simulated growth curve matching the observed growth curve (University of Wisconsin Sea Grant 1989). The dolphin model contains no term for the effect of temperature on feeding rates because the model was run assuming a constant ambient temperature

¹⁵ $CD_d = 1860$ calories·gram wet weight⁻¹; average caloric density of 4 dolphins ranging in size from 81 to 189 cm total length. Caloric density of each animal was determined as the sum of calories contained in blubber, muscle, viscera and bone divided by total animal wet weight in grams. Average caloric density of individual dolphins ranged from 1985 calories·gram wet weight⁻¹ in the 81 cm animal to 1760 calories·gram wet weight⁻¹ in the large adult female (189 cm total length). Assuming constant energy density for spotted dolphins is acceptable as spotted dolphins do not appear to exhibit any significant seasonal, and little age-related, changes in thickness of their blubber layer.

¹⁶ Energy content of diet depends on energy density of food consumed. For dolphins, this changes with age (size). Spotted dolphins nurse throughout their first year (Perrin et al. 1976). They do not begin to ingest solid food until their second year and they do not stop nursing entirely until their third year, when they are approximately 145 cm in length. In this simulation, dolphins up to 1 year of age were assumed to consume only milk (2855 calories·gram wet weight⁻¹ (Pilson and Waller 1970). Diet during the second year was assumed to consist of one-half milk and one-half adult diet (2117 calories·gram wet weight⁻¹). Diet for third year and older dolphins was assumed to be the same as that for yellowfin tunas, with an ingested energy density (CD_f) of 1380 calories·gram wet weight⁻¹.

of 37C, and this temperature was assumed to be optimum for feeding, as this is the typical mammalian body temperature.

$C_{\max}$ is the maximum possible weight-specific rate of consumption by an individual spotted dolphin at the coldest temperatures they may inhabit,

$$C_{\max} = C_a * WW_g^{C_b}$$

where $C_a^{17} = 3.98$ and $C_b^{18} = -0.29$.

Total specific rate of respiration (R_t) in the dolphin model was estimated as

$$R_t = (R_{sp} + H_d)$$

where R_{sp} is specific rate of respiration and H_d is specific rate

¹⁷Assuming maximum possible ration for adult spotted dolphins (about 75 Kg) would not exceed 15% of body weight per day (Sergeant 1969), with $C_{\max} = 0.15$, $WW_g = 85,000$ g and $C_b = -0.29$, then $C_a = 3.98$.

¹⁸ as a compromise between the unresolved arguments of Kleiber (1961; $C_b = -0.25$) and Heusner (1982; $C_b = -0.33$) for scaling of metabolic rate with size in mammals.

of residual heat loss.

Specific rate of respiration was estimated as

$$R_{sp} = (ACT_{cal} + STD_{cal} + SDA_{cal}) / CAL_{an}$$

where daily expenditure in calories for respiration is the sum of the component processes. Caloric cost of activity¹⁹ is

$$ACT_{cal} = PWR * 20650$$

where 20650 converts watts to calories·day⁻¹. Power required to swim (PWR) was estimated as

$$PWR = MP / (ME * PE)$$

¹⁹ Dolphins were assumed to swim steadily far enough below the surface to eliminate the effects of surface drag (e.g., Hertel 1966). This formulation ignores the costs of surfacing to breathe, and the attendant increase in total distance swum to follow a sinusoidal rather than a straight path through the water. Preliminary estimates of these additional costs for individual dolphins of several sizes, for reasonably realistic depths of dive and distances between surfacings ranged from 10 to 25% of steady swimming costs. As this cost is relatively low, the dolphin model was not re-formulated to include these added costs of surfacing.

where MP is mechanical power required to overcome drag, ME is mechanical efficiency²⁰ and PE is "propeller efficiency" (efficiency of propulsion by flukes)²¹. MP is estimated as a function of total drag (D_t) and velocity (VL; in centimeters·sec⁻¹) as

$$MP = ((D_t/1e^7) * VL).$$

Total drag was estimated as a function of drag due to body, fins, and movements by flukes as

$$D_t = (0.5 * N * VL^2 * S_w * C_t) / (1.0 - FID)$$

where N is density of seawater (1.025 g/cm³), S_w is wetted surface area of the body, C_t is coefficient of total drag, and FID is (fin+induced) drag. FID²² is expressed here as the fractional increase in estimated total drag due to adding the effects of fins and moving flukes.

²⁰ME = 0.20, by analogy to observed muscle efficiencies of terrestrial mammals

²¹PE = 0.85 by analogy to tunas (Magnuson 1978).

²² FID was assumed = 0.21, based on the fraction of estimated total (body + fin + induced) drag accounted for by (fin + induced) drag in the 4-dolphin sample.

S_w is wetted surface area of the body, excluding flippers, dorsal fin, and flukes, estimated as²³

$$S_w = 0.1636 * TL^{2.14}$$

Surface areas of fins are excluded from this calculation because fin drag is incorporated into the equation for total drag as an increase of 21% over drag estimated from body dimensions alone.

C_t was estimated from the formula for drag of submerged streamlined bodies moving with constant velocity

$$C_t = C_f * [1 + (1.5 * ((D_a)/TL))^{3/2} + (7 * ((D_a)/TL))^3]$$

(Hoerner 1965, Webb 1975). C_f is the coefficient of friction drag and D_a is the maximum body diameter (cm; derived from girth at axilla (G_a)) where

$$G_a = G_{aa} * WW_{kg}^{Gab}$$

²³based on measurements of wetted surface area in the 34-dolphin sample.

with $G_{aa} = 25$ and $G_{ab} = 0.28$, based on measurements of 50 spotted dolphins ranging in size from 82 to 210 cm total length.

C_f was estimated from the equation for streamlined bodies moving submerged at constant velocity in turbulent flow as

$$C_f = 0.072 R_L^{-1/5}$$

where R_L is Reynolds number, estimated here as

$$R_L = (TL * VL) / \nu$$

where ν is kinematic viscosity (equal to 0.01 Stokes) assuming turbulent flow at the boundary layer (Webb 1975) and VL is velocity ($\text{cm} \cdot \text{sec}^{-1}$), estimated as

$$VL = VL_a * TL^{VL_b}$$

where $VL_a = 20.6$ and $VL_b = 0.4$, assuming swimming velocity scales with length in the same manner for both spotted dolphins and yellowfin tuna. Using the same formula and parameters to predict velocity as a function of length in both the tuna and dolphin models maintains comparability between results from the two models. As geometrically similar swimmers, hydrodynamic constraints should be

approximately the same for both tunas and dolphins.

Specific rate of activity is then

$$ACT_{sp} = ACT_{cal}/CAL_{an}.$$

Caloric cost of standard metabolism was estimated as

$$STD_{cal} = S_a * WW_g^{S_b}$$

where $S_a^{24} = 1380$ and $S_b^{25} = 0.67$.

²⁴ S_a was assumed constant for all sizes of spotted dolphins. Given an observed rate of $0.45 \text{ mgO}_2 \cdot \text{gram wet weight}^{-1} \cdot \text{hr}^{-1}$ for a spinner dolphin (Stenella longirostris) weighing 68,000 WW_g (Hampton and Whittow 1976) and assuming $3.25 \text{ cal} \cdot \text{mgO}_2^{-1}$ (Elliot and Davidson 1975), then 2386800 ($0.45 \cdot 3.25 \cdot 68000$) calories are expended daily in standard metabolism and $S_a = 1380$ ($2386800 / (68000^{0.67})$). The observed resting rate of oxygen consumption is consistent with the range of resting rates ($0.3\text{--}0.6 \text{ mgO}_2 \cdot \text{gram wet weight}^{-1} \cdot \text{hr}^{-1}$) reported for bottlenose dolphins under various conditions (Karandeeva et al. 1973, Hampton and Whittow 1976, Hampton et. al 1971).

²⁵ Heusner (1982) presents convincing statistical arguments that intraspecific relationships between basal (standard) metabolism and body weight in adult mammals are better described by the $2/3$ power than the $3/4$ power proposed by Kleiber (1961). Heusner's argument is based on observed differences between adults of similar species (e.g., breeds of dog); but Huesner's curve is more also realistic because it predicts a relatively higher weight-specific rate in smaller (younger) animals of a given species. This is more consistent with Kleiber's (1961) observation that younger animals tend to have elevated weight-specific metabolic rates compared not only to adults of the same species, but to small

Specific rate of standard metabolism is then

$$STD_{sp} = STD_{cal}/CAL_{an}$$

Caloric cost of specific dynamic action was estimated as

$$SDA_{cal} = SDA * CONS_{cal}$$

where $SDA^{26} = 0.15$. Specific rate of specific dynamic action is then

$$SDA_{sp} = SDA_{cal}/CAL_{an}$$

adults of similar species. In young marine mammals, weight-specific standard metabolic rate is often at least twice the standard rate of adults (Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982). The parameterization above results in weight-specific estimates of S that are 2.3 to 1.3 times higher in dolphins ranging in size from 80 to 140 cm TL, than in adult dolphins (approximately 190 cm TL). This differs by 0% to 11% (increasing with increasing size) from basal metabolic rates of juvenile through adult seals of similar weight (Ashwell-Erickson and Elsner 1981).

$^{26}SDA = 0.15$, the assumed fraction of food energy converted to heat during digestion by spotted dolphins of all sizes. SDA is primarily a function of the protein content of ingested food, and is approximately 15% for a variety of carnivores, including sea otters eating clams and squid (10-13%, Costa and Kooyman 1984), harp seals eating fish (17%, Gallivan and Ronald 1981) and various terrestrial mammals fed a mixed diet (Kleiber 1961).

Specific rate of residual heat loss (H_d ; heat lost in excess of that generated by active and standard metabolism, and specific dynamic action)²⁷ was estimated as

$$H_d = H_u - (ACT_{sp} * (1.0 - ME) + STD_{sp} + SDA_{sp})$$

where $H_d > 0$, otherwise $H_d = 0$.

where H_u , ACT_{sp} , STD_{sp} , and SDA_{sp} are daily specific rates of unavoidable passive heat loss, activity, standard metabolism, and specific dynamic action, respectively. The term $(1.0 - ME)$ in conjunction with ACT_{sp} expresses the fraction of total active metabolism that is dissipated as heat rather than converted to mechanical energy. The term H_d was taken to be zero when the estimate of H_d yielded a negative result. In this case, all passive losses were more than offset by heat generated by metabolism.

²⁷ Because spotted dolphins are warm-blooded relative to their environment and because their blubber layer is not a perfect insulator, they will constantly lose heat to surrounding water. If the sum of estimated heat production generated by muscle activity, standard metabolism and specific heat of digestion equals or exceeds this unavoidable passive loss, the term has no effect. Otherwise, the additional heat loss was added to the animal's energy cost. In practice, the influence of the term was negligible, as differences between H_d and the sum of STD , ACT and SDA were less than 10%.

Unavoidable passive heat loss (H_u) is estimated as described by Brodie (1975) for passive losses in large whales

$$H_u = \frac{((21.18/BD_a) * (37.0 - T_a) * S_m / 10000.0) * 24}{WW_g * (CD_d / 1000.0)}$$

where BD_a^{28} is average blubber depth, 37.0 (C) is the assumed core temperature for spotted dolphins (Hampton and Whittow 1976), T_a is ambient temperature (assumed constant at 27C), 21.18 is the conductivity factor for whale blubber (Brodie 1975), and S_m^{29} is metabolic surface area, estimated as

$$S_m = 0.84 * S_w.$$

Unavoidable heat loss from fins and head is assumed negligible, as blood flow to these areas can be adjusted to minimize or maximize heat loss, as needed.

²⁸ $BD_a = 0.65$ cm, based on measurements of blubber depth at maximum girth for a sample of 72 spotted dolphins ranging in size from 80 to 190 cm total length.

²⁹ S_m is the surface area of the body beneath the blubber layer. S_m averaged 84% of S_w in the 4-dolphin sample.

Specific rate of waste loss (WL_{sp}) for spotted dolphins was estimated as

$$WL_{sp} = (F_a + U_a) * (CONS_{cal}/CAL_{an})$$

F_a and U_a are the fractions of calories consumed that are lost again as either solid or liquid waste³⁰.

Specific rate of growth (G_{sp}) was calculated as

$$G_{sp} = C_{sp} - (R_t + WL_{sp}).$$

Total grams wet weight biomass available daily for growth (G_{wwg}) is this specific rate times the weight of the dolphin, i.e.,

$$G_{wwg} = G_{sp} * WW_g$$

³⁰ Together these processes probably account for 15 - 20% of ingested food energy in spotted dolphins, as found for other small marine mammals eating fish (Shapunov 1973, Ronald et al. 1984, Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982, and references therein). Here, $F_a = 0.125$; $U_a = 0.07$.

Each day (i)'s new weight is simply

$$WW_{g(i)} = WW_{g(i-1)} + G_{wwg(i-1)}.$$

Unlike the tuna model, $WW_{g(i)}$ does not have to be adjusted here for prey caloric density as this factor was incorporated in the consumption portion (C_{sp}) of the model.

MODEL EVALUATIONS

Yellowfin Tuna Model

Consumption. Model estimates of consumption rate in yellowfin tunas ranged from 6.5% body weight per day in early age II fish (3310 g) to 3.4% per day in late age III fish (38,000 g). These estimates compare favorably with rates of 5-6% per day for age II and age III yellowfin, reported for several different methods of determining feeding rates of yellowfin tunas in situ (Olson and Boggs 1986).

Active metabolism. Daily cost of swimming (active metabolism) accounted for 30% to 50% of the total energy budget of four tagged yellowfin ranging in size from 87 to 96 cm (Carey and Olson 1982; in Olson and Boggs 1986). Yellowfin this size swim on average 100-130 cm/sec in situ (Holland et al 1990). Estimated daily cost of swimming steadily at 120 cm/sec in the yellowfin model comprised

36-42% of the total energy budget.

Growth. Simulated growth curves matched closely observed growth curves of yellowfin when parameter values presented in the model description were used for the terms in each of the process equations (Figure 1). This close correspondence between observed and simulated curves did not occur when other less reasonable values were used for process parameters.

Dolphin Model

Consumption. Model estimates of daily rations for spotted dolphins ranged from 9% body weight per day in first year animals to 6% in large adults. These estimated rates encompass observed rates reported by Sergeant (1969) and Van Dyke and Ridgeway (1977) for captive cetaceans. Reported observed maintenance rations for adult small cetaceans approximately the size of adult spotted dolphins are 4% to 6% of body weight per day; daily rations for smaller and younger animals can be as high as 12-15% per day.

Rations of wild dolphins have not been measured. Gaskin (1982) suggests that rations in situ may be much lower than measured in captive cetacea, but the suggestion is based on the propensity of a single species of small whale (Beluga) to gain excessive weight in oceanaria. Other species gain weight if overfed, but most maintenance rations for captive cetacea are not

lower than reported by Seargent (1969) or by Van Dyke and Ridgeway (1977) (in Ridgway and Fenner 1982).

Active metabolism. Estimated active metabolism (energy cost of swimming) ranged from 51-53% of total estimated consumption for all sizes of dolphins. Estimated standard metabolism ranged from 28-30%. Thus, dolphin model predictions conform to the convention that total metabolism of animals under field conditions is usually 2-2.5 times greater than standard (basal) metabolism (e.g., Wiegert 1976), with the majority of the increase due to activity, the rest to heat of digestion (specific dynamic action; SDA).

Standard metabolism. Standard metabolic rates estimated from the simulation model for spotted dolphins are comparable to 1) standard metabolic rates of large seals comparable in weight to spotted dolphins, 2) oxygen consumption rates of several small marine mammals, and 3) age-related changes in oxygen consumption observed in growing seals.

Standard metabolism (STD) as defined in this paper refers to resting, postabsorptive animals. Ronald et al. (1984) and Lavigne et al. (1982) report rates of "net available energy" (NE) in seals. NE refers to metabolism minus 17% estimated due to SDA. Unlike STD, NE includes the cost of routine activity in addition to basal (standard) metabolism. Ronald et al. (1984) report NE of about 145 Kcal/animal/hr for 80 Kg and 85 kg juvenile seals and a 168 Kg grey

seal. Lavigne et al. (1982) estimated NE of about 215 Kcal/animal/hr available to harp seals. Assuming routine activity added 50-100% to standard (basal) rates (Lavigne et al. 1982), standard rates (NE) for these seals were about 75-100 Kcal/animal/hr. This is similar to model estimates of standard metabolic rate of 106 Kcal/animal/hr for adult spotted dolphins (75 kg total wet weight).

Estimated standard metabolic rates, expressed in oxygen rather than energy units, are comparable to resting or basal rates reported for a variety of small marine mammals (Karandeeva et al. 1973, Hampton and Whittow 1976, Hampton et. al 1971). Model estimates for dolphins ranging in size from 5 to 90 kg wet weight ranged from 1.0 to 0.45 mgO₂/gram wet weight/hr., compared to resting rates of 0.3-0.6 mgO₂/gram wet weight/hr) reported for adult bottlenose dolphins under various conditions (Karandeeva et al. 1973, Hampton and Whittow 1976, Hampton et. al 1971). Only the data from Hampton and Whittow (1976) were used to parameterize the equation for standard metabolic rate; model estimates of STD are independent of all other reports.

The decrease in model estimates of weight-specific standard metabolic rate with increasing age of spotted dolphin to adult rates about half the neonate rate, is similar to changes in basal metabolic rate observed during maturation of many mammals (Whittow 1987, Kleiber 1961, Brody 1945) including Bering Sea harbor and

spotted seals (Ashwell-Erickson and Elsner 1981). These seals grow through approximately the same weight range as spotted dolphin, from a few kilograms as neonates to about 75 kg as adults. Observed basal metabolic rates in harbor seals ranged from 0.6 to 1.1 $\text{mgO}_2/\text{gram wet weight/hr}$, compared to estimated rates in spotted dolphin spanning the same weight range (5-75 kg wet weight) of 0.5 to 1.1 $\text{mgO}_2/\text{gram wet weight}$.

All these comparisons are general; exact comparisons are questionable because experimental, environmental, and physiological conditions differed between experiments or were ill-defined. But enough measurements have been reported to establish these rates as reasonable general expectations for standard (basal) metabolic rate of relatively inactive animals. The correspondence between these rates and rates estimated by the bioenergetics model is encouraging.

Growth. Predicted growth curves for spotted dolphins matched observed growth curves quite well when parameter values were as given in the model description (Figures 2 and 3). As with the tuna model, predicted growth curves were sensitive to parameter choice, matching observed curves poorly when parameter values were unreasonable (i.e., different from those used in the model description).

Unavoidable heat loss (H_u). Many of the parameters used in the simulation model are estimated, or chosen by analogy to other animals. Estimating H_u provides an independent check on these other estimates. If H_u is substantially greater than the sum of the estimated heat produced by standard and active metabolism, plus SDA, then something has been miscalculated. In practice, this term contributed little to estimated total flux. The sum of S, M, and SDA generally balanced H_d within 10%, using the parameters described in the methods section.

In addition, two other sets of data imply that estimated passive heat losses are reasonable. First, estimated surface heat losses are similar to observed and measured losses from other small cetacea. Second, daily rations required to replace these losses fall within the range of rations required by small captive cetacea.

Surface heat loss can be estimated as hourly heat loss divided by total surface area; model estimates range from 162 to 237 Kcal/m²/hr for spotted dolphins ranging in size from 80 to 190 cm total length. These rates are comparable to estimates of surface heat loss from other small cetaceans. Kanwisher and Sundes (1966) and Parry (1949) estimated surface heat losses of 194 and 260 Kcal/m²/hr from harbor porpoise (Phocoena). Hampton et al. (1971) measured heat flux from various surface sites on a 156 Kg bottlenose dolphin (Tursiops truncatus) and found losses of about 240 Kcal/m²/hr from the ventral trunk, 60 Kcal/m²/hr from the

lateral trunk near the head, and 10-80 Kcal/m²/hr from appendages.

Two possibilities were ignored in the estimates of minimum unavoidable (passive) heat loss; 1) the body beneath the blubber layer may not be uniformly 37C and 2) heat loss from appendages may not be negligible. If portions of the body are less than 37C, actual heat loss will be less than estimated. If heat loss from appendages is appreciable, actual heat loss will be greater than estimated.

Studies of internal temperature imply that most of the body core of Stenella in tropical water is within 1-2C of 37C. McGinnis et al. (1972) implanted temperature transmitters under the skin (but above the blubber layer) in the midventral body wall of an adult spinner dolphin (Stenella longirostris). Temperature there varied little from 35C under any conditions. Deep body temperature remained nearly constant at 37.5 C. Average body temperature beneath the blubber will lie between these limits. The large volume of (heat-generating) muscle and viscera compared to the relatively restricted and insulated metabolic (dissipative) surface implies that average body temperature integrated over the entire metabolic volume will be closer to the upper limit than the lower.

Reports of measured heat loss from appendages exist but are extremely variable (Kanwisher and Sundes 1966, Hampton et al. 1971) and apparently under control by the animal. Passive heat loss is

not entirely eliminated from appendages even during excessive cooling (McGinnis et al. 1972) but losses can be quite low (10 Kcal/m²/hr; Tursiops truncatus; Hampton et al. 1971).

Swimming Speed of Dolphin Schools

Although the dolphin schools speeds are estimated from relatively few and coarse data, estimates of the potential cost to neonates of sustaining adult speeds imply that the speed of the schools may in fact be constrained by energetics to the apparent observed speeds. Estimated daily rations for neonates sustaining adult swimming speeds were unrealistically high (> 15% body weight/day). Sustaining these speeds in neonates generates also unrealistically high estimates for daily ration of the nursing mother traveling at the same speeds (8-10% body weight/day).

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Figure 1. Observed and simulated growth curves for yellowfin tunas in the eastern tropical Pacific Ocean.

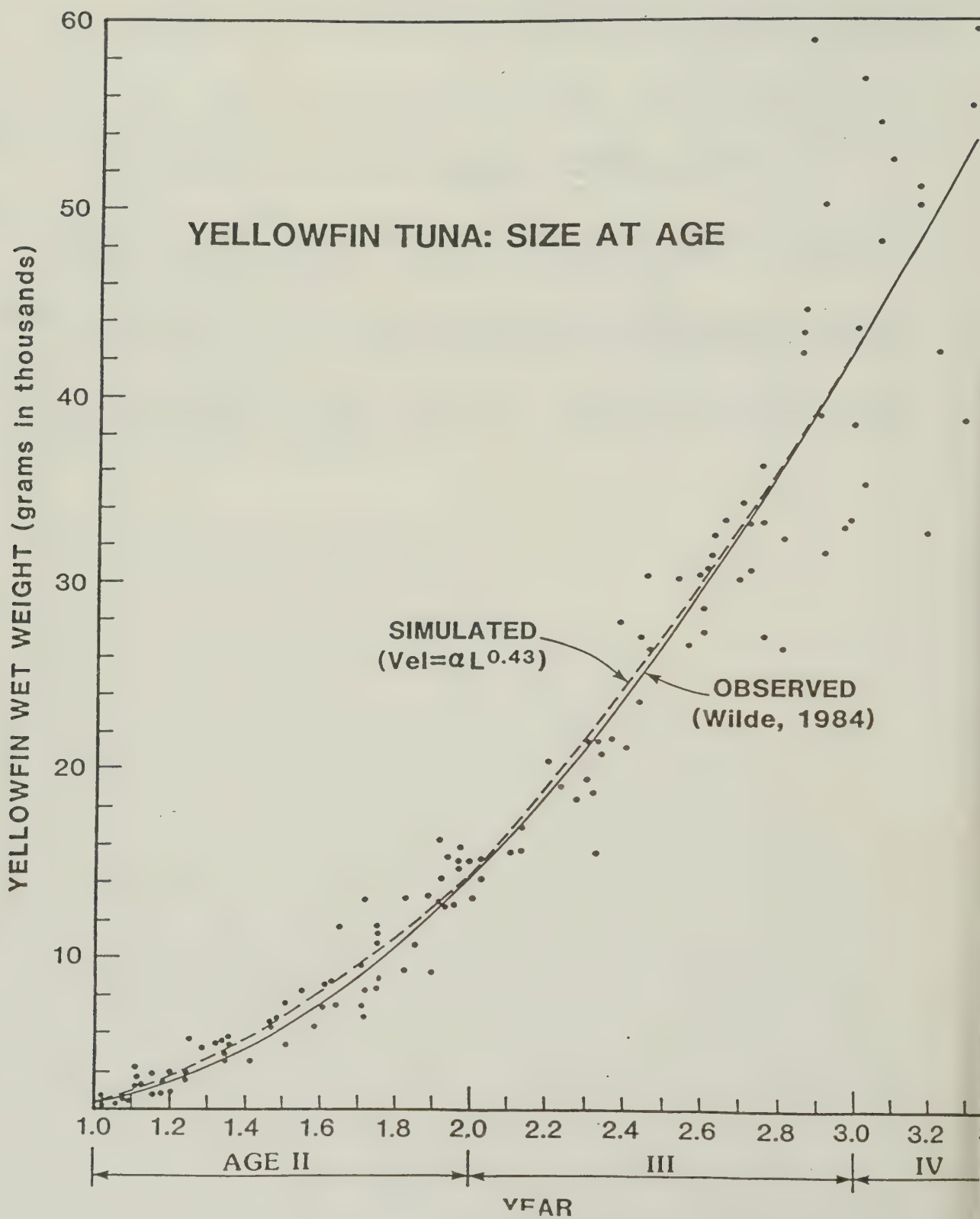


Figure 2. Observed and simulated growth curves during the first year of life for spotted dolphins in the eastern tropical Pacific Ocean.

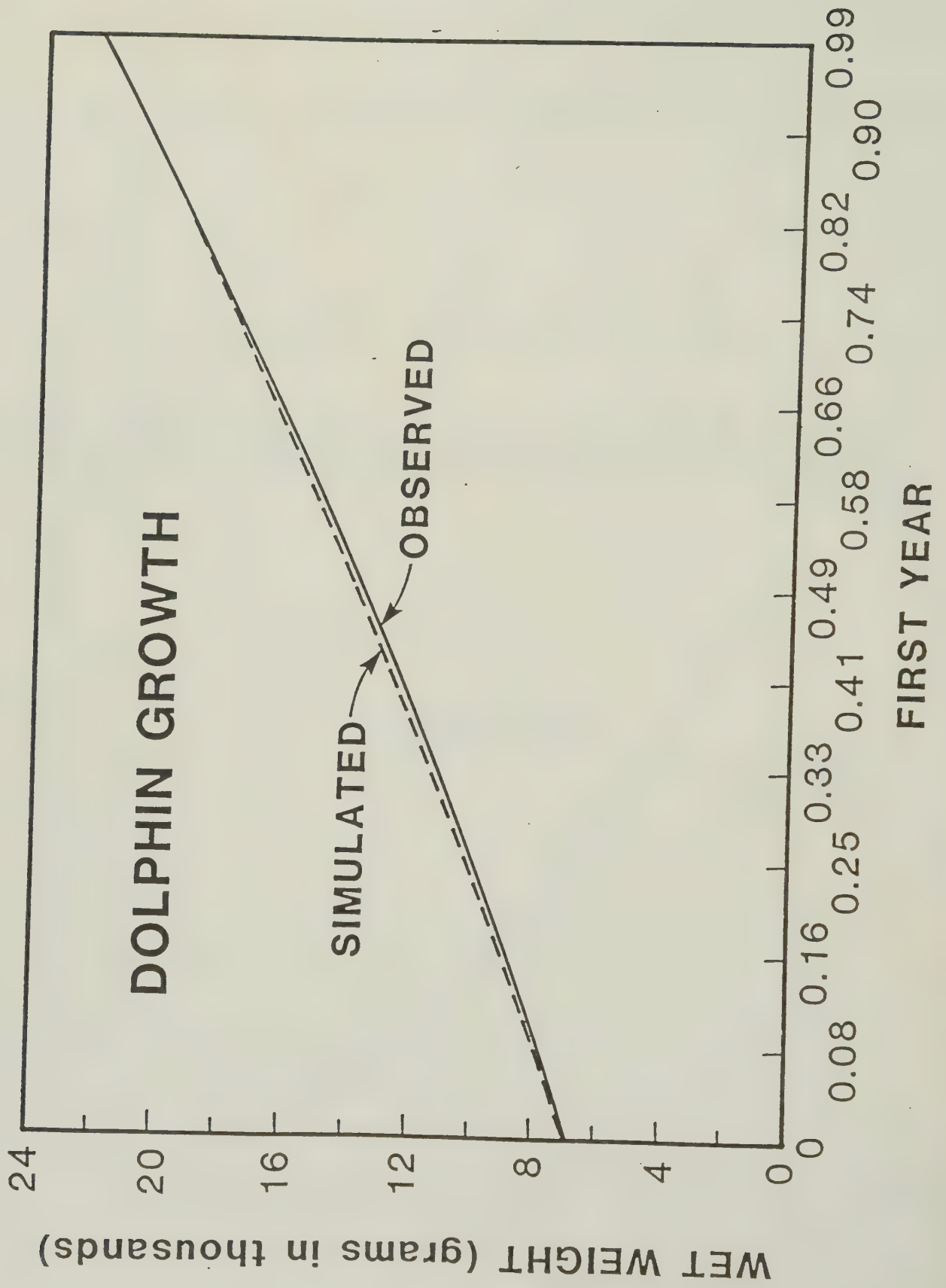


Figure 3. Observed and simulated growth curves from the second year onward for spotted dolphins in the eastern tropical Pacific Ocean.

